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A TAXONOMIC REVISION OF THE PERITRICH CILIATE GENERA *THURICOLA* AND *PSEUDOTHURICOLA*

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ABSTRACT

This paper is a critical revision of the protozoan genera *Thuricola* and *Pseudothuricola* (Ciliata, Peritrichia, Vaginicolidae). *Thuricola* Kent, 1881, is considered to include the nominal genus *Thuricolopsis* Stokes, 1887, but it is kept apart from *Pseudothuricola* Kahl, 1935. An annotated list of the hitherto described nominal species is given. Eleven species are recognized within the genus. A short description of each of these and a key to their identification are given. All recognized species are figured; some illustrations from the literature have been redrawn and brought together to facilitate comparison among them and to justify the taxonomical decisions which have been taken.

INTRODUCTION

The aim of this paper is to provide both the general reader and the specialist in peritrichs with a functional classification of the known thuricolas. There are no types of *Thuricola* species (see Corliss, 1972, table I) and, therefore, revisionary work has to be done based on information in the literature and one's own specimens. The information from the literature is first given in a formal manner with the description of each species. A checklist of the species which have been described as new is also given, just as Noland & Finley (1931) did for *Vorticella*.

Pseudothuricola is a monotypic genus. It has been included here because of its similarity with *Thuricola*.

A selection of drawings from the literature has been brought together with originals, to enhance the usefulness of this paper for specialists and general biologists.

SYSTEMATICS

Taxonomic position of the genus Thuricola

Phylum: Protozoa Goldfuss, 1818, emd. von Siebold, 1845
Subphylum: Ciliophora Doflein, 1901
Class: Ciliata Perty, 1852
Subclass: Peritrichia Stein, 1859
Order: Peritrichida Stein, 1859
Suborder: Sessilina Kahl, 1933
Family: Vaginicolidae de Fromentel, 1874
Genus: *Thuricola* Kent, 1881

The rather traditional classification above may have to be changed soon; for example, there is widespread support for recognition of the Ciliophora as an independent phylum (see Corliss' masterwork, 1979). However, I still believe that my classification is a practical one, and, for the sake of constancy, I prefer it to more recent ones. For a

brief justification of my decision, see Trueba (1978).

Diagnosis

Thuricolas are peritrichs which live as single cells or as a pair of cells. Part of their body is enclosed in a lorica or case, which stands without a stalk on the substrate. Inside the case and attached to it, there is a membranous valve which closes when the animal retracts into the lorica. In other respects *Thuricola* is a genus very similar to *Vaginicola*.

General biology of the known species

Thuricola is a genus with no aberrant species: all thuricolas look much alike. The description which follows therefore fits all known species, unless stated otherwise. *Thuricola elegans* is much smaller than the other species: this should be remembered when the sizes of different structures are indicated.

In the peculiar terminology developed for peritrichs, an unattached cell with rudimentary oral ciliature that is able to swim rapidly by means of an aboral ciliary girdle is called a telotroch. Telotrochs should not be confused with microconjugants, which are smaller and unable to build a lorica. *Thuricola* elotrochs are approximately oval in shape and about 70 μm long. They are rarely seen in nature, because as soon as they have found a suitable place they attach themselves to it and metamorphose. Telotrochs cannot feed themselves. Thuricolas attach themselves to submerged plants and debris. They do not attach themselves to animals and avoid artificial substrates (cfr. Küsters, 1934, p. 188).

As soon as it is attached to its substrate, the telotroch begins to construct its case, tube or "lorica, as these tubes are absurdly called" (Slack, 1867, p. 205). "Lorica" is a poor term indeed for the tube of thuricolas and other vaginicolids, but it is time-honoured and well established by now: I use it indiscriminately to mean tube or case. A lorica is constructed in the manner described by Vávra (1963) for *Cothurnia* sp. and by Finley and Bacon (1965) for *Pyxicola nolandi*. The lower part of the case is laid down first. It seems that the material which makes this part of the lorica

is exuded through the whole aboral surface of the ciliate. Some time later, the telotroch changes its shape, becoming more slender (fig. 5a), and the aboral ciliature is absorbed. The case grows rings of newly laid down material (fig. 5c), which seems to be shaped by the peristomial collar. After the case is finished, the adoral ciliature unfolds and the cell elongates to its normal shape (about 300 μm long).

In nature, building a lorica takes only a short time in the lifespan of the animal. I draw this conclusion because I have only twice observed the process of case-building, whereas I have seen hundreds of mature cells. When the lorica is just finished, a thuricola could be taken for a vaginicola. In fact, there is no other reason to separate the genera than the shutting valve, which I shall now describe.

The closing valve is characteristic of the genera *Thuricola* and *Pseudothuricola*. It has been described at length by Gruber (1880, pp. 463-464) and Penard (1914) pp. 24-27). Their descriptions are correct but incomplete, and like all other descriptions in the literature, they are not satisfactory when compared to the living thuricolas. There is a lot of variation among the valves: sometimes they are almost invisible (fig. 3c) and other times they are easily seen (fig. 2g). They are often double (fig. 4c), but sometimes single, just as described and figured by Penard. The variation does not seem to be species-specific. I am not aware of any recorded observations on the mode of construction of the valve, but I have seen that it takes less than a day after completion of the tube. After cell fission, the valve seems to disappear for a while. The mechanism which closes the valve has not been satisfactorily explained as yet; the fact that the cell bodies are often seen to be pinched in by the valve or valves (see for instance fig. 4c) implies that they are kept tense while the animals are feeding.

Vegetative division has been beautifully described by C. J. Muller (1869): it was a pleasant surprise for me to find my own observations already described in such an old paper. The division is unequal, of the kind usually found among peritrichs.

Sexual division has been described by Penard

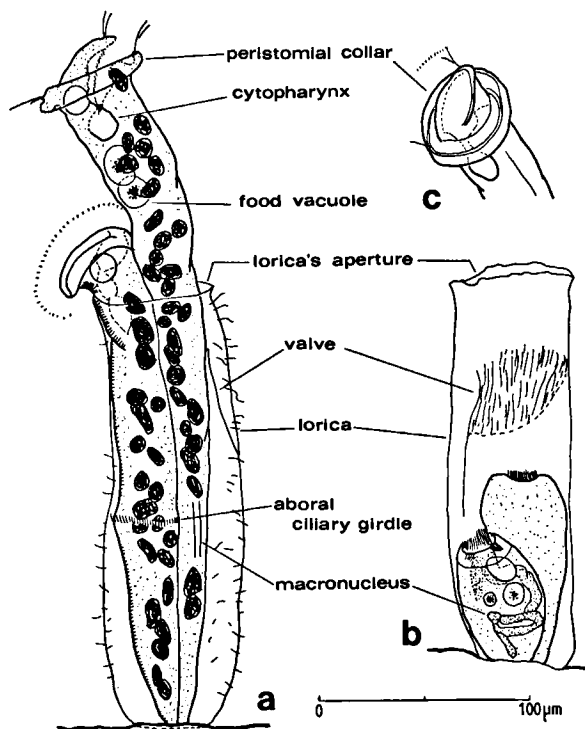


Fig. 1. Three specimens of *Thuricola innixa* attached to reed rootlets, illustrating some of the morphological terms used in this paper. a. Cells extended and feeding. The left one bears an incipient aboral ciliary girdle. Both cells are filled with bright green algae, while the case bears many filamentous bacteria on its surface. The valve is seen from the side. b. Cells contracted. The closed valve is in latero-frontal position. Internal organelles have been drawn in the shortest cell. c. Adoral zone of a feeding cell. The vibrating membranelles are scarcely visible. All specimens were freshly mounted on a glass slide and drawn by means of a prism fixed to a Zeiss interference contrast microscope (Nomarski optics). All drawings by the author have been made in this way.

(1922, p. 288). It is also a typically peritrichous process.

There are usually one or two zooids inhabiting a lorica, but some authors claim to have seen more. Empty cases are not common, for thuricolas prefer to stay in their closed loricas rather than flee from disturbances. However, they are not such extreme "homelovers" as pyxicolas, for one of the two cells living in a case may leave it by becoming a telotroch.

The contractile vacuole is placed high in the body, very near the short vestibulum, under the peristome.

Thuricolas often contain symbiotic algae (fig.

1a), which give them a beautiful bright green colour.

The (macro-)nucleus is long, flat, ribbon-like, and irregularly extended over the greatest part of the cell body; but in *T. elegans* it is said to be short, sausage-like and transversely situated.

The micronucleus, as I have observed it, is small, oval in shape, and lies near the base of the cell body (figs. 3e and 4a). Other structures are much like those of other vaginicolids.

The most similar genus to *Thuricola* is *Pseudothuricola* and thereafter *Vaginicola*.

Synonymy

- Thuricola* Kent, 1881, p. 718; Stokes, 1888a, p. 64 (key); Stokes 1888b, p. 253 (mentioned only); Kahl, 1935, p. 784; Kudo, 1947, p. 691 (and other editions of the book); Sommer, 1951, p. 410; Noland, 1959, p. 293 (key); Corliss, 1961, p. 154 (mentioned only); Matthes & Wenzel, 1966, pp. 99-110; Stiller, 1971, pp. 213-214; Pennak, 1978, p. 73; Corliss, 1977, p. 131 and 1979, p. 276 (mentioned only).
- Cothurnia* Entz, 1884, pp. 424-428; Blochmann, 1886, p. 84; Bütschli, 1889, pp. 1769-1770; Entz, 1904, pp. 140-141; Lepsi, 1926, p. 87 (key only); Schoenichen, 1927, p. 263; (all of them in part).
- Thuricolopsis* Stokes, 1887, p. 250; Stokes, 1888a, p. 64 (key); Stokes, 1888b, p. 253; Kudo, 1947, p. 691 (and also other editions).

Thuricola was erected as a genus by Kent (1881) in which to allocate the vaginicolids without a stalk but with an internal shutting valve. The valve distinguishes *Vaginicola* species from *Thuricola* species. There has been a lot of discussion in the past as to whether the valve is a reliable taxonomic characteristic. Entz (1904) went so far as to classify cothurnias, thuricolas and pseudothuricolas as one "species", which he called *Cothurnia crystallina*. I do not agree with him. Variation in vaginicolids may be great in some respects but not to the extreme of missing an organelle like the valve of thuricolas. In my experience thuricolas can be recognized as such and distinguished from vaginicolids and cothurnias even before seeing the closing valves (which they very seldom fail to have). The genus *Thuricola* includes animals with and without a stalk inside the lorica. Considering the variability of the internal stalk, I

think it is unreasonable to divide the genus further solely on the basis of stalk length.

The general approach to the genus *Thuricolopsis* has been to ignore it. It is indeed a poorly defined genus. Its author erected it because of the presence of "an internal, narrow, flexible valve-rest to receive and support the descended valve" in some species. As stated in the description of the genus, it is easy to make incorrect interpretations of the shutting mechanism and this probably happened with Stokes. In my opinion the genus *Thuricolopsis* should not have been erected and it should not be used any more; Corliss (1979, p. 208) rejects the name also. The situation of *Pseudothuricola* is quite different. I have kept it apart from *Thuricola*, for reasons which are explained below.

Taxonomic characteristics

Easy as it is to characterize the genus because the species of *Thuricola* are so similar, it is difficult to classify specimens into species by a single characteristic because they are so variable. Information on the pellicular striae is not given in the literature, or given very ambiguously. Most often the substrate is a plant. The stalk, which varies in form, apparently has no function. Nonetheless, there are two characteristics which may be used for identification, namely the habitat and the shape of the tube. By habitat, I mean the nature of the aquatic environment. In this paper freshwater and saltwater species are treated separately; I believe that the salinity of the water in which the animals are found is a reliable and convenient characteristic to work with. However, brackish water organisms remind us that there may be species of *Thuricola* that are able to live in both kinds of water.

The shape of the lorica is the dominant feature used for classifying thuricolas and, indeed, vaginicolids in general. There are nonetheless different opinions about the varied shape of the loricas. We have seen that Entz (1904) lumped together several genera into one species; Kahl (1935, p. 785) says of *T. folliculata* that its lorica shape is very constant; Sommer (1951, p. 411) calls *Thuricola* a very difficult genus. Penard (1922, p. 286) states that the tube is "très constante de forme et

de structure", but that it has not been realized that each lorica should be studied from two sides, not only from one point of view. I believe Penard was quite right: since the loricas are not purely cylindrical, it is confusing to look at only one side of them. Unfortunately, most descriptions of thuricolas (including many of my own) are based on the aspect of the specimen seen from one side only. It is impractical to draw specimens 90° around their long axis; but a good idea of the shape of the tube can be gained by measuring its width at two or three points (aperture, midpoint and maximum width) by using the focusing micrometer on the microscope. With all its limitations, the shape of the lorica is useful as a taxonomic characteristic, and has the advantage that it can be studied on contracted and fixed specimens.

Staining techniques and the electron microscope have not been used for this study. It is possible that they could add taxonomically valuable information to our knowledge, but as yet there are no publications on the study of thuricolas using such techniques, and I preferred to limit myself to the traditional methods, with the exception of using Nomarski interference contrast optics. When dealing with ciliates which lack stable structures such as shells and loricas, a study of the "silver line system" like Foissner's (1976) may prove necessary, but otherwise it is easier to put up without it.

To facilitate discussion, the following terms are used unequivocally throughout this paper: lorica, case and tube mean the same; shape quotient means the quotient of the length (of the lorica) divided by the width.

Remarks on nomenclature

The same remark has to be made for *Thuricola* as has been made for *Pyxicola*: according to article 30 (a) (2) of the International Code of Zoological Nomenclature, *Thuricola* should be treated as being of feminine gender. No attempt should be made to change the spelling of the old feminine specific epithets into masculine ones, or to give masculine names to new species.

Key to species

Eleven species are recognized in this paper. They can be identified with the aid of fig. 2 and the following key.

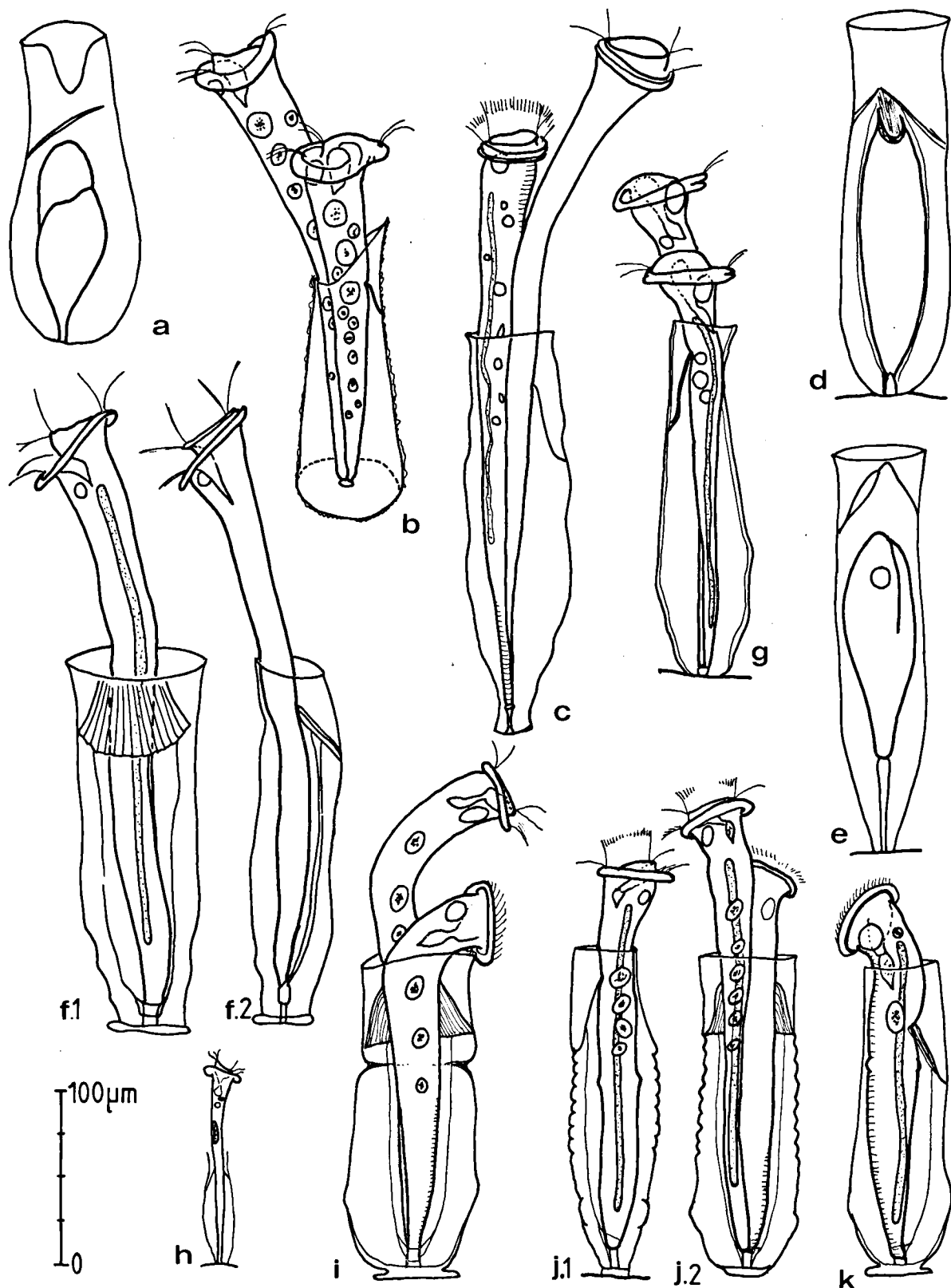


Fig. 2. Representative specimens of the species recognized in this paper. The drawings have all been taken from the literature, and reproduced on the same scale, to facilitate comparison. As in all other figures in this paper, the original drawings have been reproduced in scale with the aid of an electronic pantograph respecting the style of the original authors. Sometimes, the figures are simplified, but never "corrected". a. *Thuricola incisa* after Daday. b. *T.*

vasiformis, after Hamman. c. *T. similis*, after Bock. d. *T. innixa*, after Vejdovsky. e. *T. kellicottiana*, after Stokes (1882). f. *T. folliculata*, after Kahl (1935): f.1: broad side view; f.2: from the narrow side. g. *T. gracilis*, after Sommer. h. *T. elegans*, after Biernacka. i. *T. constricta*. j. *T. obconica*: j.1: narrow side; j.2: broad side. k. *T. valvata*. i-k after Küsters.

- 1.a. Fresh water (less than 2‰ salinity) 2
- b. Salt or brackish water 7
- 2.a. Edge of the lorica with an indentation, inferior part inflated *T. incisa* (fig. 2a)
- b. Aperture not indented 3
- 3.a. Lorica resembling an Erlenmeyer flask, its base much broader than the aperture
..... *T. vasiformis* (fig. 2b)
- b. Lorica approximately cylindrical in shape 4
- 4.a. Lorica pointed at the base, circular in cross section; living in sewage *T. similis* (fig. 2c)
- b. Lorica pointed or not pointed at the base, circular or oval in cross section; living in oxygenated, much cleaner waters 5
- 5.a. Lorica circular in cross section, nearly cylindrical in shape, rounded at the base, stalk short or absent *T. innixa* (fig. 2d)
- b. Lorica circular or elliptical in cross section, but not cylindrical in shape, pointed or rounded at the base; viewed from the narrow side the diameter of the aperture is less than elsewhere in the lorica; stalk longer than 10 μm *T. kellicottiana* (fig. 2e)
- c. Lorica elliptical in cross section 6
- 6.a. Viewed from narrower side, the lorica is cylindrical, somewhat pointed at the base; aperture as wide as the rest of the lorica, stalk shorter than 10 μm ... *T. folliculata* (fig. 2f)
- b. Viewed from the smaller side, the lorica has a small neck, and is not pointed at the base; the aperture is narrower than the inferior part of the lorica; stalk short or absent
..... *T. gracilis* (fig. 2g)
- 7.a. Tube shorter than 100 μm *T. elegans* (fig. 2h)
- b. Tube longer than 100 μm 8
- 8.a. Tube rounded at the base, with a clear constriction above the middle
..... *T. constricta* (fig. 2i)
- b. Tube without deep constriction; several shallow undulations may be present 9
- 9.a. Tube rounded at the base, aperture almost circular, 120-190 μm long *T. valvata* (fig. 2k)
- b. Tube tapering towards the base, aperture elliptical, 150-220 μm long *T. obconica* (fig. 2j)

The species

The recognized species, with their synonyms, are described below, in the same order as they appear-

ed in the key; often the "diagnosis" is followed by additional "remarks". After each reference, an indication on the source of the information contained in the referred publication is given: (orig.) means original information present in that publication.

Thuricola incisa (von Daday, 1910) n. comb.

Cothurnia incisa von Daday, 1910, p. 27, pl. I, fig. 13 (orig., but see the remarks below) (fig. 2a of this paper).

Diagnosis. — Lorica 160-180 μm long, rounded at the base; the aperture is round in cross section but its edge is vertically indented.

Substrate. — The algal colonies of *Microcystis aeruginosa*.

Habitat. — The fresh water lake of Victoria (Africa); found only once, but this does not mean it is uncommon; the sessile ciliates of Africa have not yet been studied.

Remarks. — Von Daday studied material that was fixed, but abundant, according to him. It is very difficult to decide whether or not the author intended to draw a stalk in the original drawing; the printed figure in the publication (von Daday, 1910) is not sharp enough.

The name and first description of *C. incisa* appear in von Daday (1910); in that publication the author does not label this species as "sp. nov.", but gives a reference to an earlier paper of his (von Daday, 1905 (probably appeared in 1906)). However, this earlier paper does not mention *C. incisa*. Probably due to error, Daday thought that he had described *C. incisa* before.

Thuricola vasiformis Hammann, 1952

Thuricola vasiformis Hammann, 1952, pp. 219-220, fig. 21 (orig.) (fig. 2b of this paper); Nusch, 1970, p. 33 (orig.); Stiller, 1971, p. 251, fig. 130c (from Hammann).

Diagnosis. — Lorica 160 μm long, widest at the base (59 μm) and round in cross section. It resembles a small Erlenmeyer bottle. Stalk very short.

Substrates. — Debris. It attaches also to microscope slides.

Habitat. — Beta-mesosaprobic water of a pond.

Thuricola similis Bock, 1963

Thuricola similis Bock, 1963, pp. 91-96, fig. 1-2 (orig.) (see fig. 2c of this paper).

Diagnosis. — Lorica 158-248 μm long (mean 183 μm), cylindrical in shape, but tapering slightly towards the base. Aperture 45 μm in diameter. Stalk 10-20 μm long. The lorica wall is not smooth, but somewhat irregular, with undulations.

Substrate. — Bacterial matter.

Habitat. — Activated sludge found only once.

Remarks. — Fig. 2 of the original paper is composed of four microphotographs showing some of the variation found in this species. *T. similis* is the only thuricola that has been found in polluted waters.

Thuricola innixa Stokes, 1882

Planicola folliculata de Fromentel, 1874, pl. 9 fig. 2 (orig., see the remarks below.)

Thuricola innixa Stokes, 1882, pp. 182-183, fig. 38 (orig.) (fig. 3a of this paper); Kahl, 1935, p. 786, fig. 145, 12 (from Stokes).

Thuricola Gruberi Vejdosky, 1892, pp. 52-57, 1 pl. (orig.) (fig. 2d of this paper).

Thuricola valvata Kent, 1881, p. 718, pl. 40, figs. 4-5 (in part) (partially from Wright); Maskell, 1887, p. 13 (record only); Dalla Torre, 1891, p. 203 (record only); Stokes, 1888a, fig. 13 (from Wright); Stokes, 1888b (mentioned only).

Cothurnia regalis Penard, 1914, pp. 58-59, pl. 3, figs. 1-8, pl. 5, figs. 8-10 (orig.).

Thuricolopsis innixa Stokes, 1887, p. 251, fig. 16 (mostly from Stokes, 1882); Stokes, 1888a, fig. 14 (no text) (from Stokes, 1882); Stokes, 1888b, pp. 253-254, pl. 9, fig. 11 (from Stokes, 1882).

Vaginicola (unnamed): Warner, 1870, pp. 33-34, fig. 43 (orig.).

Diagnosis. — Lorica 140-200 μm long, evenly cylindrical in shape, circular in cross section (not compressed), rounded at the base; stalk short but more frequently absent.

Substrate. — Algae and water plants, including mosses.

Habitat. — Fresh water; not as common as *T. folliculata*.

Remarks. — As this species closely resembles *Thuricola folliculata*, I have been tempted to combine both species. But, after considering Kahl's statement on *T. folliculata*: "Die Form des Gehäuses ist so konstant, dass ein Verkennen gar nicht möglich ist", and my own experience, I think these two species should indeed be distinguished from each other.

Nonetheless, one may find a few specimens which are difficult to identify. The nominal spe-

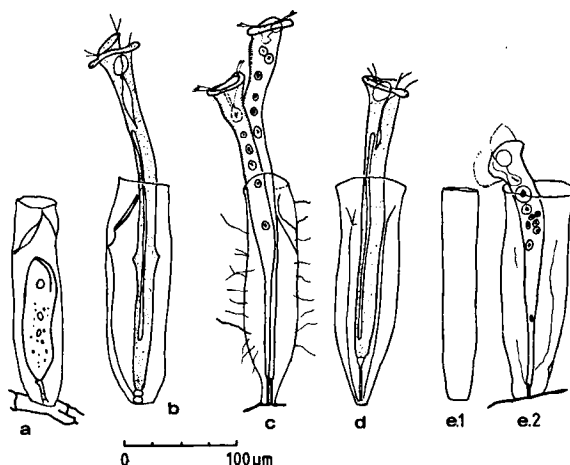


Fig. 3. Three fresh water species of *Thuricola* very similar to each other. a. *T. innixa*, after Stokes (1882). b. "*Cothurnia regalis*", a synonym of the preceding species, after Penard (1914). c. A specimen of *T. kellicottiana* viewed from the narrow side, attached to a reed rootlet. The tube is covered with bacterial threads. d. "*Cothurnia castellensis*", a synonym of *T. kellicottiana*, after Penard (1914). e. *T. folliculata*, attached to a reed rootlet: e.1: sketch of the tube in lateral view, made from depth measurements of the animal as seen under the microscope in the position shown in the next figure. e.2: Viewed from the broad side. Note the micronucleus in the lower part of the cell and the barely visible membrane around the cell body. This transparent sheath is all that can be seen of the shutting apparatus.

cies "*Planicola folliculata*" is here attributed to de Fromentel, as it was published in his book (1874), but it should be noticed that the title-page of that book bears the note "Planches et notes descriptives des espèces per Mme. J. Jobard-Muteau". This kind of co-authorship may explain some of the repetitions and discrepancies found in that work.

Thuricola kellicottiana (Stokes, 1887) Kahl, 1935

Thuricola innixa sensu Kellicott, 1884, p. 120, pl. 3 fig. 5 (orig.).

Thuricola Kellicottiana Kahl, 1935, p. 785, fig. 145, 5-6, 11 (from Penard and Stokes); Nusch, 1970, p. 33, fig. 33 (orig.).

Thuricola amphora Sommer, 1951, pp. 410-411, pl. 20 fig. 36 (orig.); Stiller, 1971, p. 214, fig. 131 C (from Sommer).

Thuricola (unnamed figure): Corliss, 1979, pl. 29 fig. 85 (from Sommer).

Thuricolopsis Kellicottiana Stokes, 1887, p. 251, fig. 17 (orig.; fig. 2e of this paper); Stokes, 1888, p. 254, pl. 9 fig. 12 (from Stokes, 1887).

Cothurnia crystallina sensu Entz, 1904, pp. 140-141 (in part), fig. 10g.

Cothurnia castellensis Penard, 1914, pp. 59-60, pl. 3, figs. 9-11, 13-14, pl. 5, figs. 11-12 (orig.) (see fig. 3d of this paper).

Cothurnia Kellicottiana Penard, 1922, p. 290, fig. 272 (from Penard, 1914).

Diagnosis. — Lorica 170-230 μm long (usually about 200 μm), circular or slightly elliptical in cross section, widest diameter in the lower half of the lorica, which tapers to the base. Stalk thin, longer than in other thuricolas, 7-15 μm long.

Substrate. — Algae and other water plants.

Habitat. — Fresh water; common.

Remarks. — This form is quite easy to distinguish from other thuricolas, even though Nusch has seen many intermediates between it and *Thuricola folliculata*. I have also seen some intermediate forms but it is usually easy to classify them as the "folliculata" or the "kellicottiana" form. Nusch stated (p. 23) that this species should be regarded as a morphological variant of *T. folliculata*, although he himself treats it as a separate species.

***Thuricola folliculata* Kent, 1881**

Planicola folliculata de Fromentel, 1874, p. 248, pl. 3, fig. 13 (pl. 9 fig. 2 is possibly *T. innixa*).

Thuricola folliculata Kent, 1881, pp. 718-719, pl. 40, figs. 6-8 (orig.; the figures do not look life-like); Kahl, 1935, p. 785, figs. 142, 41; 145, 1-2 (fig. 2f of this paper), 4 (orig.); Kudo, 1947, p. 691, fig. 325e (from Kahl) (other editions omitted here); Matthes, 1950, p. 447 (orig.); Sommer, 1951, pp. 411-412, pl. 21 figs. 37a-b (orig.); Hamman, 1952, p. 218 (orig.); Noland, 1959, fig. 10, 32d (from Kahl); Liebmann, 1962, pp. 379-480, fig. 413, pl. 14 fig. 32 (orig.); Matthes & Wenzel, 1966, p. 100, fig. 73e (from Sommer); Nusch, 1970, pp. 31-32, fig. 32 (orig.); Stiller, 1971, p. 214, figs. 130 A-B (from Kahl); Bick, 1972, pp. 128-129, fig. 66 (from Kahl, retouched); Streble & Krauter, 1973, p. 250, fig. p. 39, 27, fig. 251, 3 (orig.) (pl. 14 is probably *T. gracilis*).

Thuricola obliqua Sommer, 1951, p. 413, pl. 20 fig. 39 (orig.); Stiller, 1971, p. 216, fig. 131A (from Sommer).

Thuricola (unnamed figures): Pennak, 1978, fig. 46H (orig.?). Corliss, 1979, pl. 29, fig. 84 (from Sommer).

Cothurnia crystallina sensu Steinecke, 1940, p. 111, fig. 69.5 (after Reukauf; I have not found the original).

Diagnosis. — Lorica 126-236 μm long, usually about 180 μm . The shape of the case is that of a compressed cylinder which tapers a little towards the base. Widest diameter at the aperture. Viewed from the broad side it resembles *T. gracilis*, but is more slender; from the narrow side it looks quite different from *T. gracilis*, more like *T. innixa*. Stalk short or absent.

Some individuals are intermediate between *T. folliculata* and *T. kellicottiana*.

Substrate. — Submerged plants.

Habitat. — Beta-mesosaprobic fresh waters; common.

Remarks. — The specific epithet "folliculata" was given by Kent to some of his thuricolas because he thought that Müller's (1786) *Vorticella folliculata* was the same kind of organism. After carefully reading Müller's description (pp. 285-286, no figs.), I have come to the conclusion that, whatever it was, the creature that Müller wanted to describe was not a thuricola. Müller says that *Vorticella folliculata* looks like a *Trichoda inquilinus*, and that is certainly not a thuricola (see his figures: 1788, pl. 9 fig. 2). Furthermore, Müller maintains that *V. folliculata* is to be found on *Cyclops* sp., and we do not know as yet of an epizootic thuricola. Dujardin (1841, p. 564) identifies *V. folliculata* with *Cothurnia imberbis* Ehrenberg,

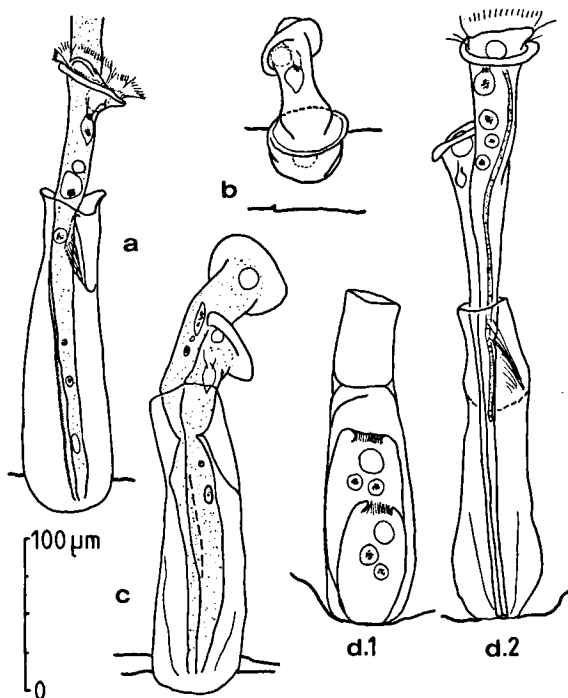


Fig. 4 Four specimens of *Thuricola gracilis* viewed from different angles. a. Seen from the narrowest side. The longest cell has been drawn only in part. b. Viewed from above. Note the elliptical aperture. c. In this specimen both cells are pinched by the shutting valve. d. Two views of the same specimen. Note the constriction of the tube. 1. Contracted. 2. Extended: note the very short stalk on which the cells stand.

and this seems to me a more convincing interpretation than Kahl's.

The figures given by Kent (pl. 40, figs. 6-8) are not abnormal as far as the cell body is concerned, but the tube looks quite strange, not life-like: he drew those figures from memory, probably wanting to emphasize the closing valve. Nevertheless the name *Thuricola folliculata* is by now so well established that I prefer to let it stay as it is. The best description given of this species is that of Kahl (1935).

Thuricola gracilis Sommer, 1951

Vaginicola aquatica valvata Slack, 1867, pp. 205-207, figs. 1-3 (orig.).

Cothurnia valvata D'Udekem, 1864, pp. 27-28, pl. 5, figs. 2a-b (orig.).

Cothurnia crystallina sensu Entz, 1904, pp. 140-142 (in part) fig. 10e; Penard, 1922, pp. 285-290, figs. 268-271 (in part; orig.).

Thuricola folliculata sensu Streble & Krauter, 1973, pl. 14 (orig. photomicrograph).

Thuricola gracilis Sommer, 1951, pp. 412-413, pl. 20, fig. 38 (orig.; fig. 2g of this paper); Stiller, 1971, pp. 214-215, fig. 131 B (from Sommer).

Thuricola pediculata Sommer, 1951, pp. 413-415, pl. 22, fig. 40 (orig.); Corliss, 1979, pl. 29, fig. 85.

Thuricola viridis Sommer, 1951, p. 415, pl. 22, figs. 41a-b (orig.); Hammann, 1952, p. 220 (orig.).

Diagnosis. — Lorica 140-220 μm long, usually about 180 μm . Viewed from the narrow side, the shape of the lorica is characteristic for the species: base rounded, widest diameter near the base, tapering towards a bottle-neck near the aperture; often asymmetrical. From the broad side, the lorica looks rectangular, tapering slightly towards the base. Stalk short or absent.

Substrate. — Algae and other water plants.

Habitat. — Mesosaprobic fresh waters; common.

Remarks. — Fig. 268, 3 in Penard (1922) leaves no doubt about the identification of some of his "*Cothurnia crystallina*" with *T. gracilis*. He did not consider it as separate species, however.

From the three names given by Sommer to what I think are specimens of the same species, I have chosen *T. gracilis* because it is the first described in her publication, it conforms best with my own observations and its name is the most appropriate, as it underlines the gracefulness of the organism.

Symbiotic algae are often found in thuricolas (see for example fig. 1a), as stated in the general

description of the genus; *T. viridis* is just such a specimen of *T. gracilis*.

Thuricola elegans Biernacka, 1963

Thuricola elegans Biernacka, 1963, pp. 62-63, fig. 140 (orig.; fig. 2h of this paper).

Diagnosis. — Lorica 65 μm long, widest at its middle, somewhat constricted at the superior part. Stalk very short or absent. Macronucleus very short, only 8 μm in the original drawing.

Substrate. — Algae.

Habitat. — Found only once in brackish water (7‰ salinity) of the Baltic Sea.

Remark. — Although only described in brief, the small size and the peculiar macronucleus make this animal distinct enough to be retained as a separate species.

Thuricola constricta Küsters, 1974

Thuricola constricta Küsters, 1974, pp. 188-189, fig. 23 (orig.; fig. 2i of this paper).

Diagnosis. — Lorica 160-174 μm long, 62-70 μm wide, aperture 60-67 μm ; laterally compressed (elliptical in cross section), rounded at the base. It bears a single, clear-cut constriction above its middle with the closing valve invariably attached above it. Stalk very short.

Remarks. — There are doubts as to whether this species is really different from *T. valvata*. I have kept it as a separate species because its author claims to have seen several of them (p. 175) and they were all equally constricted.

Thuricola valvata (Wright, 1858) Kahl, 1933

Vaginicola valvata Wright, 1858, p. 279, pl. 6 figs. 6-7 (orig.).

Cothurnia operculata Gruber, 1879, p. 518-519 (orig.); Gruber, 1880, p. 462-464, pl. 26 figs. 29-32 (orig.).

Thuricola operculata Kent, 1881, p. 719, pl. 40 figs. 13-15 (from Gruber).

Cothurnia valvata Dons, 1922, pp. 64-65, figs. 12-14 (orig.).

Thuricola aestuarii Biernacka, 1963, p. 62, fig. 130 (orig.).

Thuricola valvata Kahl, 1933, p. 135 fig. 24.16; Kahl, 1935, p. 786, figs. 142, 42-43 (from Gruber); 145.3 (orig.). Dons, 1948, p. 10, fig. 12 (orig.); Bock, 1952, p. 227, fig. 1 (orig.); Felinska, 1965, p. 238, fig. 2H (orig.); Küsters, 1974, pp. 189-190, fig. 24 (orig.) (fig. 2k of this paper).

Diagnosis. — Lorica 120-190 μm long, rounded at the base, slightly elliptical in cross-section; aper-

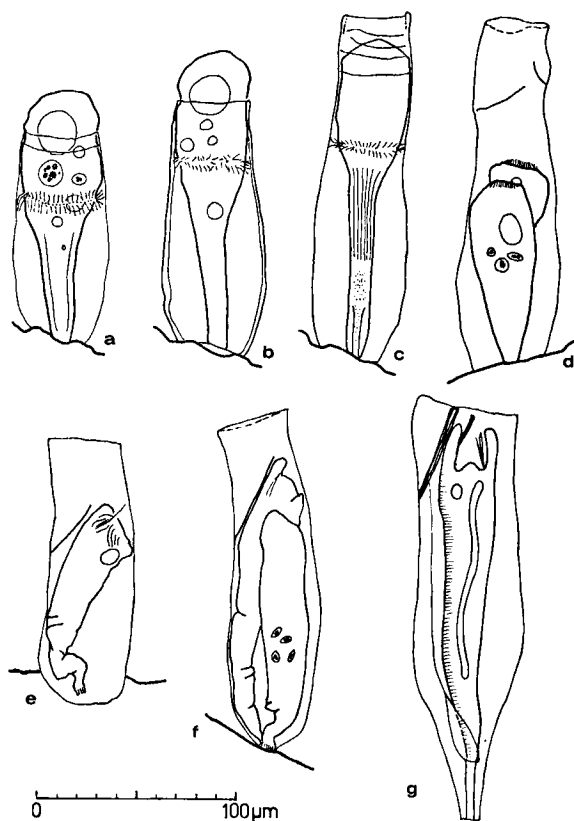


Fig. 5. Above (a-d): the building of the tube by a specimen of *T. gracilis*. a. The lorica material is very thin, especially at the top, where a circular transparent ribbon has just been laid down by the top of the cell. b. 7 minutes later, both cell and tube have grown longer. The macronucleus of the cell (not drawn) is located above the ciliary girdle. c. 45 minutes later the tube is finished. A few minutes later, the cell contracts and changes its shape into the adult form. It resorbs its posterior ciliary girdle and develops its adult ciliature located around the discus and down to the cytopharynx (these last changes have not been drawn). d. One day later there are two cells inside the lorica, which already has its closing valve. The extended cells look like those in fig. 4a.

Below (e-g): three marine thuricolas. e. and f. Two specimens of *Thuricola valvata* from the North Sea near Amsterdam. The cells are contracted in an irregular manner. Substrate: green algae. g. *T. obconica*, after Kahl (1933).

ture circular or almost so; shape quotient 2.8 to 4.4, usually 3.5. Stalk short or absent.

Substrate. — Algae.

Habitat. — Sea-water.

Remarks. — This species is difficult to distinguish from *T. obconica* at least until some specimens of each species have been compared with each other; see the remarks on *T. obconica* for a discussion on

their differences. The synonyms given above are assumed, because the descriptions in the literature do not allow a definite identification.

***Thuricola obconica* Kahl, 1933**

Thuricola fimbriate Kellicott, 1894, pp. 10-11 (no figs.). *Thuricola obconica* Kahl, 1933, p. II. c. 135, fig. 24.15 (orig.); Kahl, 1935, p. 786, figs. p. 785, 7-8 (orig.); Biernacka, 1963, pp. 61-62, figs. 138a-b (orig.); Küsters, 1974, pp. 190-191, figs. 25a-c (orig.) (fig. 2j of this paper).

Thuricola kamptostoma Bock, 1952, pp. 227-228, pl. 22, fig. 3 (orig.).

Diagnosis. — Lorica 150-220 μm long, tapering towards the base, sometimes truncated, elliptical in cross-section, aperture also elliptical. Shape quotient 3.5 to 4.5, usually 4. Stalk very variable: quite long (20 μm), short, or even absent.

Substrate. — Algae.

Habitat. — Salt and brackish water; common.

Remarks. — The characteristics of *T. obconica* and *T. valvata* overlap so much that it remains doubtful whether they are two different species. I am well aware that there are thuricolas which could be classified within either species with equal right. However, I understand that in general *T. obconica* has a longer and more slender case than *T. valvata*. The literature should be studied cautiously, because the drawings have mostly been made without the aid of a drawing prism, and consequently the proportions are often distorted. Compare for instance the figures of Kent (1881) of *T. valvata*, which are retouched copies, with their model, the figures of *Vaginicola valvata* in Wright (1858): the shape quotients of the loricas in Kent's drawings are lower than those in Wright's drawings. *Thuricola fimbriate* Kellicott is possibly a senior synonym, but it is difficult to be sure, because there is no drawing with the original description.

THE MONOTYPIC GENUS ***Pseudothuricola* KAHL, 1935**

Erected by Kahl in his famous monograph, *Pseudothuricola* stands in its own right as a genus which could be defined as follows: vaginicolids with erect loricae which are fixed to the substrate by external stalks; similar in all respects to *Cothurnia*, but bearing inside the tube a membranous

valve which occludes the aperture like that of a *Thuricola* species.

It is of course a matter of opinion whether *Pseudothuricola* should be retained as a separate genus. I prefer to do so for several reasons: 1) Structurally it differs as much from the other genera of the vaginicolids as for instance *Cothurnia*; 2) To include *Pseudothuricola dyonisii* either in the genus *Cothurnia* or *Thuricola* would make these genera heterogeneous; 3) The number of species of vaginicolids (including *Pseudothuricola* spp.) will probably increase rather than diminish. Corliss (1979: 276) retains the name also.

***Pseudothuricola dyonisii* (Penard, 1914) Kahl, 1935**

Cothurnia crystallina sensu Entz, 1904, pp. 140-141 in part, figs. 10d (fig. 6a of this paper) and fig. 10f (orig.).

Cothurniopsis Dyonisii Penard, 1914, pp. 61-62 in part, pl. 2 figs. 17-22 (from which figs. 6c-d of this paper has been taken), pl. 5 figs. 13-14, not figs. 15-16 (orig.).

Pseudothuricola dyonisii Kahl, 1935, p. 786, fig. 145, 9-10 (from Penard); Stiller, 1971, pp. 216-217, figs. 132 A-B (from Penard).

Diagnosis. — Lorica 93-100 μ m long, laterally compressed, widest (30-35 μ m) below the middle; tapering from that point to the base; asymmetrical when viewed from the narrow side. Internal stalk short or absent; external stalk 15-20 μ m long.

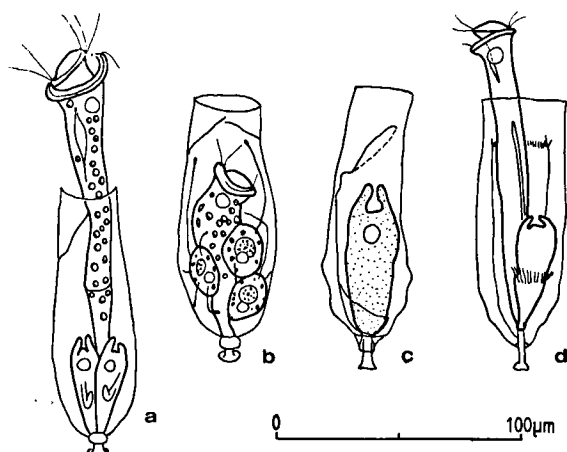


Fig. 6. The four drawings of *Pseudothuricola dyonisii* which can be found in the literature. a. An expanded specimen with 2 microconjugants. b. A specimen attacked by three suctorians. (Both a and b from Entz, 1904). c. Side view and d. view of the broad side of two other specimens. The right one holds a smaller cell at its base, probably a microconjugant, like those in a. (Figs. c and d after Penard, 1914).

Substrate. — Moss. Probably other plants as well.

Habitat. — Among mosses; found only once.

Remarks. — Penard (p. 62) describes, besides his regular *P. dyonisii*, another vaginicolid which he considers to be a variant of the first. But what he actually describes is only the case of the variant, and does not mention the valve it should bear to be classified as a pseudothuricola. Furthermore, the drawings of the "size variant" do not show a valve. For these reasons I think it was a small cothurnia.

ANNOTATED LIST OF NOMINAL SPECIES

Here below follows a list of the hitherto described "new species" of the two genera considered in this paper, with their original names. After each entry a reference is given to the name of the species of which I consider it to be synonym; more information about that nominal species is then to be found under that name in the preceding sections of this paper. An effort has been made to make the list complete and the references accurate.

Cothurnia castellensis Penard, 1914, is a synonym of *T. kellicottiana*, as its own author stated in a later publication (1922).

Cothurnia incisa von Daday, 1910 is regarded as a valid species in this paper. See *T. incisa*.

Cothurnia regalis Penard, 1914 was extensively deported in a preliminary note, and then well described with drawings in a full-length paper. I consider this name to be a synonym of *T. valvata*.

Cothurnia regalis penard, 1914 was extensively described by its author. In 1922, Penard considered it to be synonym of what he calls *C. crystallina*. I think *C. regalis* is a synonym of *T. innixa*.

Thuricola aestuarii Biernacka, 1963 is insufficiently described. I have classified it as a synonym of *T. valvata*.

T. amphora Sommer, 1951 is a synonym of *T. kellicottiana*.

T. constricta Küsters, 1974 greatly resembles *T. valvata*, but following the assertion of its author, I also consider it to be a genuine species.

T. elegans Biernacka, 1963 is a distinct species, if

one takes its small dimensions into consideration. *T. fimbriate* Kellicott, 1894 was reported without figures to illustrate the description. Now this name is a *nomen oblitum* for *T. obconica*.

T. folliculata Kent, 1881 was not reported as a new species because its author identified it with *Vorticella folliculata* Müller, 1786. I do not think Müller's description applies to a thuricola: see the remarks on *T. folliculata* for a discussion on this subject.

T. gracilis Sommer, 1951 was first described by Penard as *Cothurnia crystallina*, but Sommer gave it the name and status of a new species.

T. Gruberi Vejdovsky, 1892, described in a paper difficult to find, has been ignored as an available name. It is well described, but the name is a junior synonym of *T. innixa*.

T. innixa Stokes, 1882 seems to be the valid name of the species.

T. kamptostoma Bock, 1952 is most probably a junior synonym of *T. obconica*.

T. obconica Kahl, 1933 was first described very briefly; but later, Kahl (1935) published some more information on it. I consider it a valid species.

T. obliqua Sommer, 1951 looks too much like a somewhat distorted *T. folliculata* to be considered a species in its own right. I have seen several such *T. folliculata* specimens. In fact I have even made them by gently pressing onto the coverglass of my microscopical preparation. Compare *T. obliqua* with *Planicola inclinata* de Fromentel, 1874 (pp. 248-249, pl. 7 fig. 17).

T. pediculata Sommer, 1951: a synonym of *T. kellicottiana*.

T. similis Bock, 1963 has been described as living on activated sludge. This fact, together with its morphological characteristics make this species distinct enough, since no other thuricola is known to live in dirty waters.

T. vasiformis Hammann, 1952 is a distinct species.

T. viridis Sommer, 1951 looks peculiar in the original drawing, but I do not think it is more than a *T. gracilis* with many symbiotic algae within the cell body.

Thuricolopsis Kellicottiana Stokes, 1887, discovered by Kellicott (1884) is in this paper called *Thu-*

ricola kellicottiana but it should be noted that the intermediate forms between this species and *T. folliculata* have been described.

Vaginicola valvata Wright, 1858 is a misspelling or an unnecessary correction of *Vaginicola valvata*. It was the first thuricola to be described. See *Thuricola valvata*.

Vaginicola aquatica valvata Slack, 1867 is the name given to a single and damaged specimen. The drawing of the organism is not enough to identify it with certainty, but I think it is a specimen of *T. gracilis*.

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